

ECOLOGICAL ADAPTIONS OF A FRESHWATER SPONGE ASSOCIATION IN THE RIVER RHINE, GERMANY (PORIFERA: SPONGILLIDAE)

JOCHEN GUGEL

Gugel, J. 1999 06 30: Ecological adaptations of a freshwater sponge association in the River Rhine, Germany (Porifera: Spongillidae). *Memoirs of the Queensland Museum* 44: 215-224. Brisbane. ISSN 0079-8835.

The species composition and autecology of freshwater sponges (Porifera, Spongillidae) were investigated in the Rhine between Karlsruhe and Bonn (Germany) between 1993 and 1995. *Ephydatia fluviatilis*, *E. muelleri*, *Trochospongilla horrida*, *Spongilla lacustris*, *Emmapius fragilis* and *E. carteri* were found. *Ephydatia fluviatilis* was classified as an r-strategist due to its high ability to colonise new habitats, whereas other species placed emphasis on successful establishment in more stable habitats and should therefore be classified as K-strategists (among freshwater sponges). Similarly, the production of larvae was an integral part of the life cycle only in *E. fluviatilis*, whereas other species put their main efforts in producing gemmules as distribution-units. Asexual vs. sexual reproductive strategies in freshwater sponges in running-water habitats is discussed in terms of their prevalence, periodicity and influence of limnological factors. □ *Porifera, Spongillidae, life cycle, adaptations, central Europe, running water, river Rhine.*

Jochen Gugel (email: jochen@post.tau.ac.il), Darmstadt University of Technology, Institute of Zoology, Schnittspahnstrasse 3, D-64287 Darmstadt, Germany. Present address: Tel Aviv University, George S. Wise Faculty of Life Sciences, Department of Zoology, Ramat Aviv, Tel Aviv 69978, Israel; 15 March 1999.

A considerable number of publications on life cycles of freshwater sponges are now available (e.g. Gilbert et al., 1975, Frost et al., 1982, Courrèges & Fell, 1989, Bisbee, 1992). Mostly these focus on single life cycle events, such as formation of larvae or gemmulation, and often include only a single species. Only a few papers deal with associations of several species, their colonisation strategies and spatial competition (e.g. Williamson & Williamson, 1979; Mukai, 1989; Pronzato & Manconi, 1991). The present investigation reports on five sympatric species occurring in the Rhine between Karlsruhe and Bonn (Germany), their reproductive strategies and colonisation.

At the beginning of the 20th century Lauterborn distinguished 83 macrobenthic animals in the Rhine (Tittizer et al., 1990). In the 1970's these numbers decreased to 12 species (Conrad et al., 1977), due to an extremely high level of pollution. Since that time great efforts have been undertaken to purify the water, and the number of macrobenthic animals has again risen steadily (Schöll et al., 1995). This species diversity now exceeds that of Lauterborn, whereas the species composition is not the same as in the beginning of the century (Tittizer et al., 1990), due to the huge changes in the Rhine. In recent years ongoing invasions of foreign species (Neozoa:

Kinzelbach, 1995) have been taking place, and have influenced the biocoenosis considerably.

Results of Franz (1992) indicate that the Rhine is a highly suitable habitat for sessile filter feeders. Not only is the nutritional situation excellent for these animals due to its eutrophic waters, but the banks are entirely covered by rocks which provide a suitable substrate. Filter feeding is not restricted to sessile animals - in particular many insects also gain their nutrition from filter feeding - and Mann et al. (1972) stated that the productivity of filter feeders is extremely high within waters disturbed by anthropogenic influences.

Nevertheless, our knowledge about freshwater sponges in the Rhine is still fragmentary, despite regular, general studies on the macrobenthic fauna. Such studies usually include sponges, although they are often given only cursory considerations.

This seems surprising since repeatedly high abundances of single species have attracted the attention of researchers in the past (Schön, 1957; Bartl, 1984). Large rivers are characterised by unpredictable changing water levels. This offers and destroys new habitats - a situation which seems difficult to deal with for sessile organisms.

TABLE 1. Collecting sites and dates of collections Key: 1, Near the facilities of the BASF AG. 2, Outflow of the cooling water circuit of the power plant, the temperature is here up to 10°C higher than the surrounding river. 3, Slightly polluted stagnant water. *, Collection undertaken with a grab dredger on board of the research ship 'Argus'.

Locality	22-23.i.93	08-11.v.93	24-26.viii.93*	7-8.ix.93*	25-26.ix.93	6-7.xi.93	22.ii.94	11.v.94*	8.vi.94*	30.vi.94*	15-26.vii.94*	10-11.viii.94	14-15.x.94	15.iii.95	3.viii.95	8.x.95	12-14.x.95
Iffezheim																	x
Neuburg	x	x										x					x
Leimersheim	x	X										x					x
Sondernheim	x	x										x					x
Altrip	x	x										x					x
Ludwigshafen ¹	x	x										x					x
Lampertheim-Rosen-Garten					x	x	x				x		x	x	x	x	
Worms				x													x
Biblis, nuclear power plant ²					x	x					x		x	x	x		
Biblis, downstream n.p.pl.						x					x						
Worms-Rheinduerk-Heim	x	x										x					X
Gross-Rohrheim											x		x	x			
Gross-Rohrheim, 2km downstream					x	x					x		x	x	x	x	
Gernsheim			x	x	x	x	x				x		x	x		x	
Kornsand			x	x		x	x		x	x	x	x	x			x	
Nierstein	x	x	x														x
Oxbow of Ginsheim ³					x	x	x				x	x	x				
Mainz-Laubenheim	x	x	x	x					x	x							x
Mainz			x	x				x	x	x							
Heidenfahrt									x			x					
Bingen	x	x						x	x			x					x
Bacharach	x	x										x					x
Boppard	x	x										x					x
Urmitz/Kaltenenger	x	x										x					x
Bad Breisig	x	x										x					x
Remagen																	x
Bonn-Bad Godesberg																	x

METHODS

COLLECTION. Samples were collected from many sites in the Rhine (Germany) (Fig. 1), with dates of collection for each site listed in Table 1. Collections were mostly made from the banks of the river, by wading in the water and removing substrate by hand. Some collections were made with a grab dredger aboard the research ship 'Argus' of the federal state Hesse (indicated with an asterisk in Table 1).

Sponges were removed from the substrate with a knife and preserved immediately in 70%

ethanol. From each individual sponge, one microscope slide was prepared.

Individual sponges growing on approximately 1.3m² available substrate at each collecting site were counted.

The average number of individual sponges per m² of available substrate were calculated (Figs 4-9). Only active colonies were counted, no dead colonies or gemmules without their living mother-sponge.

Methods of preparation for microscopy followed Arndt (1928), with slight modifications. Sponge identification was based

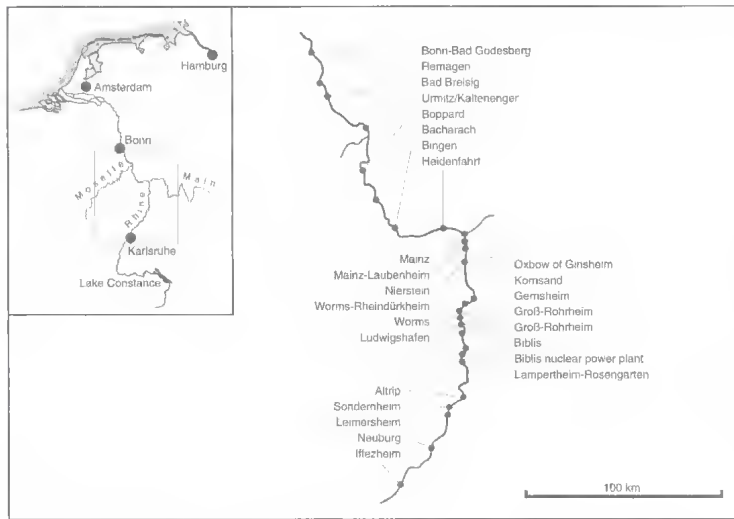


FIG. 1. Rhine collecting sites.

on Arndt (1926, 1928) and Penney & Racek (1968).

Slides prepared during this study are deposited in the Senckenberg Museum of Frankfurt (SMF).

EVALUATION OF THE PERIOD OF FLOODING BEFORE COLLECTION. At each collection site the actual water depth was recorded for all sponge samples. Daily information on water levels at the stations of Worms and Mainz were recorded (Fig. 2), thus for each site the period of flooding before collection could be calculated.

RESULTS

FAUNISTICS. Six species were found in the present study, listed according to their prevalence from abundant to rare: *Trochospongilla horrida* Weltner, 1893; *Ephydatia fluviatilis* (L., 1758); *Spongilla lacustris* (L., 1758); *Ephydatia muelleri* (Lieberkühn, 1855); *Eunapius fragilis* (Leidy, 1851); *Eunapius carteri* (Bowerbank, 1863).

SUBSTRATE. Sponges were found settling on all kind of solid substrates. Within the Rhine this mainly consists of rocks placed to support the river banks; wood is rarely found. Aquatic macrophytes are almost non existent in the investigated area, only once was a small *E. fluviatilis* found epizootic on *Fontinalis* sp. (Bryophyta, Fontinalaceae).

As a rule, the larger rocks (immovable by average currents) were more likely to be colonised with sponges. Smaller rocks (often moved by average currents) were rarely settled by sponges or other sessile organisms. These preliminary data agree with those of Rützler (1965), who studied colonisation by marine sponges in the Mediterranean Sea.

DISTRIBUTION IN RELATION TO DIFFERENT FLOODING REGIMES. The species-assemblages varied considerably between sites dependent on flooding events, comparing sites flooded more

than six months before collecting, and those flooded only nine weeks prior to collection (Fig. 3). *Ephydatia fluviatilis* was the only species occurring regularly at the more recently flooded sites, whereas at sites flooded more than six months before collecting this species had the same absolute abundance in colony-counts, but colonies grew much larger. The other species, *T. horrida*, *S. lacustris*, *E. fragilis* and *E. muelleri*, also appeared at both these categories of sites, but only in very small numbers and small size at recently flooded sites (with most having a diameter of less than 1 cm).

It was also apparent that differences in flooding events between the sites is a major factor responsible for different depth preferences of sponge species. Places recently flooded were very shallow, often dry, whereas places flooded over 6 months ago were deeper, below the levels affected during river-level fluctuations.

Other factors show no depth dependent variations in the river environment. Nutrient levels should be evenly distributed within the waterbody, due to turbulent currents, and light can only penetrate about 0.75 m through the water column due to high turbidity.

In Figure 3 and subsequent figures only colony-counts are given, where no distinction has been made according to the size or local abundance of colonies.

SEASONAL DEVELOPMENT. The general outline of the development of sponge species associations is given in Figure 4. A generalised model of a life-cycle of a freshwater sponge in the

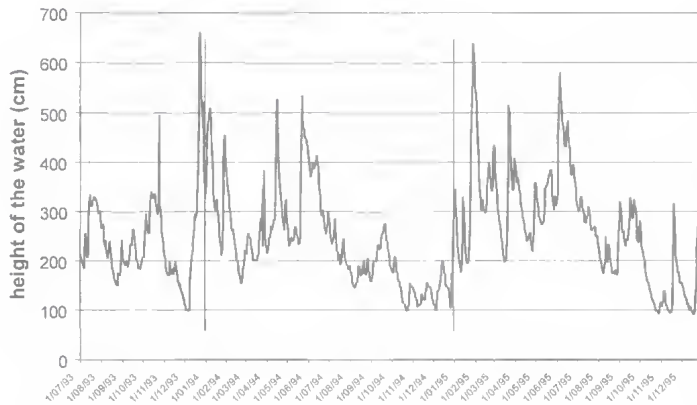


FIG. 2. The niveau of daily water levels at Worms from July 1993–December 1995; the vertical lines indicate the turn of the years (the scale is relative, without a defined zero point).

Rhine is as follows (Fig. 4). In March–April young sponges hatched from their overwintering gemmules. Sponges grew until midsummer (July–August), sexually produced larvae may occur from May to July. Asexual gemmules were produced year-round, but more regularly towards the autumn. In September–October the colonies declined and desintegrated, thus producing overwintering units (gemmules).

SPECIES AUTECOLOGY. Statements about the presence or absence of sexual reproduction usually require histological analysis of specimens, which was not conducted in this study. Under low magnification only fully developed larvae were

clearly visible, not the preceding states of larval development, but it was not the goal of this study to describe the life history of these sponges, only to report on the presence or absence of mature larvae, as important indicators on the ecology of species.

Spongilla lacustris. This species formed thick crusts (1–3 cm thick); the outline was irregular with rounded edges. Colonies could reach a considerable size (up to 1 m²). Only very few colonies showed tendencies towards branching growth forms. Colonies of *S. lacustris* always disintegrated in late autumn (October–November). In winter

(December–February) only gemmules survived. The first young sponges hatched from gemmules in spring (beginning of April), the number of colonies then rose steadily until October (Fig. 5). The high numbers of colonies reported during the period from October–December were mainly due to these colonies being present at the beginning of October, whereas by the end of October their numbers had declined rapidly. Furthermore, the larger colonies observed in October fragmented into several smaller colonies before dying, so that counts of number of colonies rose before they dropped, and eventually disappeared completely in December–March.

more than 6 months flooded

less than 9 weeks flooded

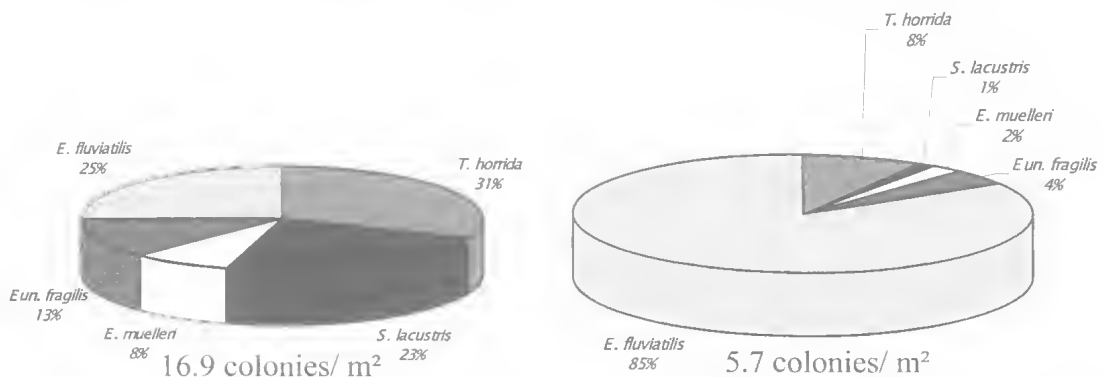


FIG. 3. Species-assemblages at places with different times of flooding before collection (numbers are calculated for 1 m²): 26 collections were made at sites more than 6 months prior to flooding of collection sites; 28 collections took place at sites less than 9 weeks prior to flooding.

TABLE 2. Life cycle data and ecological strategies of the five sympatric sponge species.

Event	<i>E. fluviatilis</i>	<i>S. lacustris</i>	<i>E. muelleri</i>	<i>E. fragilis</i>	<i>T. horrida</i>
Time of greatest abundance	October (autumn)	October (autumn)	June (early summer)	May-June (early summer)	August-September (late summer)
Overwintering units	Whole colony	Weakly fixed free gemmules	Fixed free gemmules	Attached gemmule crusts	Attached gemmule crusts
Distribution units	Larvae	Drifting gemmules	Drifting gemmules	Larvae	?
Colonisation of newly established habitats	Through active swimming larvae	Not observed	Not observed	Not observed	Not observed
Ecological strategy	r-strategy	K-strategy	K-strategy	K-strategy	K-strategy

Gemmules generally appeared from August, but their appearance seemed to be less dependent on seasonality and more dependent on colony size. This was also true for other species (see Rasmont, 1962, 1963; Simpson, 1980). Colonies of *S. lacustris* larger than 3cm in diameter always contained at least some gemmules; smaller colonies were mostly free of gemmules, at whatever time of the year they were encountered. Gemmules were built singly within the tissue of the mother-sponge, always within the basal parts of the colonies. The gemmulation process was more regular towards the end of the life span of intact colonies. There were often dense, single-layered carpets of gemmules, resting where they formed. The whole sponges disintegrated after death, but sheltered parts of the skeleton still remained intact so that gemmules resting in these patches of skeletal refugia were bound together and weakly fixed to the substrate. Green

gemmules, due to an infestation with unicellular symbiotic algae and a gemmule-polymorphism, as described by Gilbert & Simpson (1976) and Brondsted & Brondsted (1953), were not observed in this study. Larvae were not observed in this species from the Rhine. This was very intriguing given that in other habitats colonies of *S. lacustris* containing larvae were regularly found (e.g. within the outflow of the 'Steinbrücker Teich', a eutrophic pond near Darmstadt, Germany, nearly 50% of the colonies in July 1994 contained larvae).

In early autumn about 30% of colonies were bright green due to the presence of symbiotic algae (Fig. 5). Only during this part of the year were water levels low enough to provide the preferred habitats for *S. lacustris* (i.e. in slightly deeper, permanently flooded water, Fig. 3), with sufficient light for the successful photosynthesis of symbionts.

Eunapius fragilis. This species formed low crusts (1-2cm thick), with an irregular outline and rounded edges. Rarely it exceeded a diameter of 5cm. Colonies of *E. fragilis* usually disintegrated in summer (July-September). In winter (December-February) intact colonies were rarely found (Fig. 6). The first sponges hatched from gemmules in spring (April). Immediately after hatching the highest numbers of colonies appeared (Fig. 6). The species completed its gemmulation process up until summer (July), after which colonies began to disintegrate. Gemmules were formed *in situ* producing a pavement-like gemmule crust, tightly fixed to the substrate. These gemmules are virtually immovable and it is difficult to perceive how they could contribute to the dispersal within the habitat, whereas in May-June 1994 free movable larvae were found in about 10% of colonies. Colonies containing symbiotic algae were not found within the Rhine, probably because their preferred distribution was in permanently flooded,

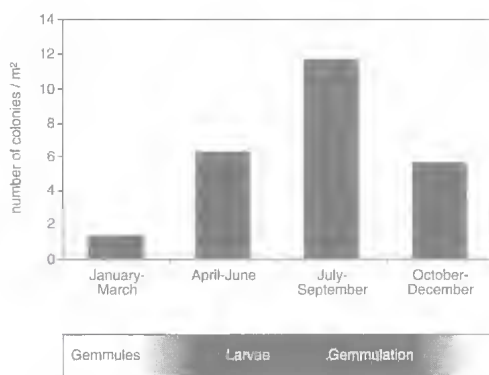


FIG. 4. Seasonal appearance of Spongillidae in general in the Rhine study sites. The white bar indicates when only gemmules are present; the black bar represents times of the year when active colonies are present; the time-scale of the chart corresponds with that of the bar.

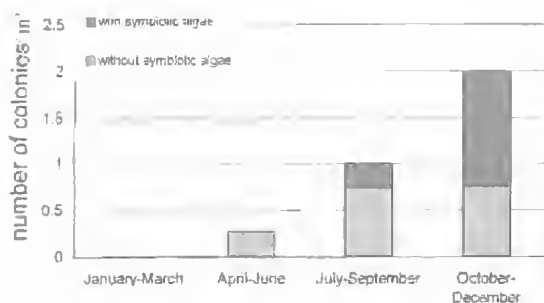


FIG. 5. Seasonal appearance and number of symbiotic colonies in *Spongilla lacustris*.

deeper habitats, where light regimes may be insufficient for photosynthesis (Fig. 3).

Eunapius carteri. This species record from the Rhine is the first time it has been encountered in central Europe (see Gugel, 1995). It was found November 1993 within the cooling-water outflow of the nuclear power plant in Biblis. A detailed description and discussion about its dispersal are given in Gugel (1995).

Ephydatia fluviatilis. This species forms more-or-less thin encrustations (1-2cm thick). Smaller colonies (less than 5cm diameter), had a circular outline, whereas larger ones (more than 7cm diameter), were more irregularly shaped. Colonies of this species grew up to 20cm diameter. *Ephydatia fluviatilis* was regularly seen alive in winter (December-February), in contrast to the other species. Overwintering colonies were small crusts, only 1.5cm diameter, in which no canal systems were visible. These probably survive in a reduced state, as suggested by Arndt (1928) and Weissenfels (1989). In early spring (April) their abundance was only slightly increased in comparison with winter (Fig. 7), probably due to hatching of gemmules (see below), whereas the number of colonies dramatically increased during June-July (Fig. 7), at which time a large-scale production of larvae

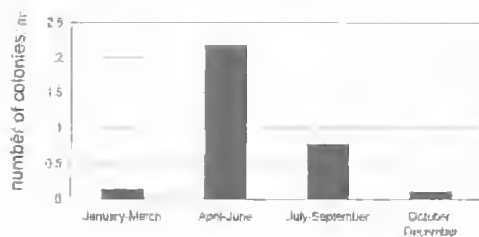


FIG. 6. Seasonal appearance of *Eunapius fragilis*.

took place (June). In July these larvae had settled and built new colonies. The gemmulation process was irregular throughout the whole year and a considerable number of colonies was always devoid of gemmules. When gemmules were present their numbers were reduced: in colonies of 5cm diameter not more than 10 gemmules were found. During fragmentation of sponges few gemmules were freed from the mother-sponge and these 'hatched' in spring. The highest number of colonies was encountered during October-December. As in the case of *S. lacustris*, the large colonies present in autumn fragmented into several smaller colonies, many of which died towards winter (December-February), the overwintering colonies were also small.

In May-June about 25% of colonies produced larvae. This seemed to be the most important event in the life cycle of *E. fluviatilis*, as in July many very small colonies were seen in close proximity to each other, a phenomenon quoted as 'Sprühinfektion' (spray infection) by Steusloff (1938). As already indicated, *E. fluviatilis* was the only species which occurred in higher numbers at sites flooded only a few weeks prior to collection (Fig. 3). This was probably due to the more active dispersal of larvae. Symbiotic colonies were never found.

Ephydatia muelleri. Colonies of this species were mostly thickly encrusting (2-4cm thick), with irregular outline and rounded edges. The diameter was rarely more than 10cm. The first colonies of *E. muelleri* appeared in spring (at the beginning of April), and soon after hatching colonies were found in large numbers, peaking during summer (July/August). After completing gemmulation colonies died, usually from the beginning of August to October (Fig. 8). Active colonies were not observed during winter (November-March), only dead colonies with gemmules. *Ephydatia muelleri* often used its entire tissue for gemmule-production, whereas its skeleton remained intact for considerable period of time after the death of the maternal sponge. Large numbers of gemmules were fixed by the skeleton to the place of production. In this way a successful recolonisation at the same site was ensured in the following year. In addition, when single gemmules became free and were no longer fixed to the substrate, they could be distributed by the current within the habitat, providing an effective mechanism for dispersal and recolonisation of adjacent habitats. Sexually produced larvae were not observed in this

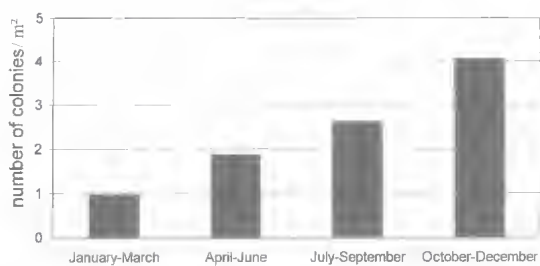


FIG. 7. Seasonal appearance of *Ephydatia fluviatilis*.

species, and only a single symbiotic colony was found (from Sondernheim, in August 1994), close to symbiotic colonies of *S. lacustris*. *Ephydatia muelleri* is mainly distributed in deeper waters, below the levels affected during river-level fluctuations (Fig. 3).

Trochospongilla horrida. Colonies of this species formed thin encrustations (less than 1 cm thick), with a very irregular outline. Large colonies may cover an area of 0.5 m². *Trochospongilla horrida* began hatching from gemmules in spring (early April). The highest abundance, in both numbers and size of colonies, was reached in summer (August; Fig. 9). In autumn (September-October) colonies always disintegrated and left the gemmule crusts tightly adhered to the substrate. As in *E. fragilis*, gemmules remain fixed to their place of production and it is difficult to imagine that they might be dispersed within the river. Gemmulation commenced in early summer (June-July), and at this time especially *T. horrida* was a successful space-competitor against the otherwise dominating neozoan crustacean *Corophium curvispinum* (Amphipoda). When growing, small colonies tended to fuse with other colonies of the same species, thus forming larger 'super-colonies'. Neither larvae nor colonies containing symbiotic algae were observed. The species was

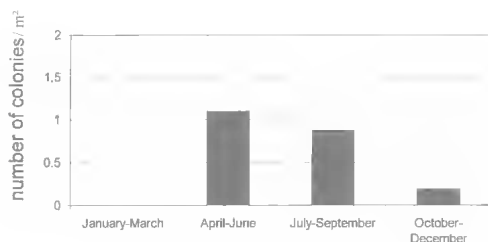


FIG. 8. Seasonal appearance of *Ephydatia muelleri*.

mainly distributed in permanently flooded habitats (Fig. 3).

Ecological strategies for each species are summarised in Table 2.

DISCUSSION

Freshwater sponges often display a considerable plasticity in their ecological strategies (Pronzato & Manconi, 1994a), and their life cycles are often adapted to the special requirements of their habitats (e.g. *E. fluviatilis* in temperate regions is usually active during summer and inactive during winter). In hot, arid regions the pattern of activity/inactivity is reversed (Harsha et al., 1983; Corriero et al., 1994). This shows that the life cycle is very adaptable to specific climatic conditions (Pronzato & Manconi, 1994b). According to Pronzato et al. (1993) the life cycle of *E. fluviatilis* seems to be controlled by exogenous factors in regions with strongly oscillating environmental conditions. In more stable habitats endogenous control seems to dominate.

For several species the data presented in the literature differ from those presented here. For example, Bisbee (1992) reported the presence of active colonies year-round in *S. lacustris* from North Carolina. He observed gemmulation in late spring-early summer, sexual reproduction in April, and some sponges disappeared during summer. According to Cheatham & Harris (1953) both *E. fragilis* and *T. horrida* were active year-round in Texas. Pronzato & Manconi (1995) counted up to 324 gemmules cm⁻² of tissue in *E. fluviatilis* from Sardinia.

Ecological strategies of these species are given in Table 2. *Ephydatia fluviatilis* is considered to be an r-strategist, mainly for its ability to colonise new habitats. In contrast, the remaining species are characterised as k-strategists because they lack this ability.

This general tendency is congruent with results of Pronzato & Manconi (1991), who compared *E. fluviatilis* and *S. lacustris* showing the former to be more successful in colonising new habitats, whereas the latter was more successful as a competitor.

Details in the life cycle of *E. fluviatilis* seem to contradict this classification as an r-strategist: the dominance of sexual vs. asexual reproduction and its year-round presence; these are usually quoted as typical for k-strategists (Pianka, 1970).

The successful colonisation of new habitats is here considered to be due mainly to active

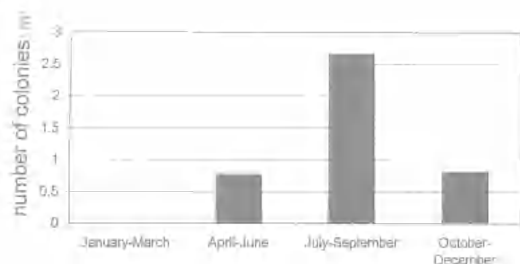


FIG. 9. Seasonal appearance of *Trochospongilla horrida*.

distribution of free larvae. The production of larvae in Spongillidae is mostly controlled by endogenous factors (Gilbert et al., 1975). The seasonal appearance of larvae is confined to a few weeks in the year, and this timing is synchronous between various localities, Leveaux (1941, 1942) reported that production of larvae in *E. fluviatilis* in central Europe is confined to May-June, which corresponds to the results presented here. Since timing in the production of larvae is severely constricted to certain weeks in the year and cannot be altered in the short term, producing larvae does not appear to be an effective strategy to react to unpredictable environmental changes.

The so-called k-strategists (*T. horrida*, *S. lacustris*, *E. muelleri* and *E. fragilis*) have the potential to produce a large number of offspring via their gemmules, traditionally an r-strategy feature. These species do produce a lot of gemmules, but these usually stay at the place of their production (see Table 2).

According to Manconi & Pronzato (1991) *S. lacustris* follows the r-strategy in the short-term, but is essentially a k-strategist in the long term. In many Spongillidae both strategies occur simultaneously (Pronzato & Manconi 1995), even within the same structures: the gemmules serve as distribution-units under an r-strategy, and as resting bodies under a k-strategy.

It was surprising to see that asexual reproduction was clearly dominant over sexual reproduction. Larvae were only observed in *E. fluviatilis* and to a lesser degree in *E. fragilis*.

In the special limnological environment of running water it must be questioned whether or not gemmules are more suitable distribution-units than larvae, aside from their role as resting bodies. They are more robust than larvae, and dispersal is passive via currents. There is no need

or advantage in having a capacity for active dispersal.

Van de Vyver & Willenz (1975) reported that in *E. fluviatilis* from Belgium sexual reproduction is confined to overwintering colonies. In that species the development of oocytes commenced in autumn of the year prior to larval production, which occurred the following June. In Belgium, parts of colonies of *E. fluviatilis* survived winter as living, but reduced colonies, similar to the Rhine populations. These results are also confirmed by Weissenfels (1989). Williamson & Williamson (1979) discussed whether or not sexual reproduction was triggered by a pheromone in Spongillidae. According to these authors sexual reproduction occurs rarely in running water because the postulated pheromone would be diluted and ineffective (in contrast to situations in stagnant water). This hypothesis would explain the occurrence of many larvae in colonies of *S. lacustris* within the outflow of the 'Steinbrücker Teich' (see above), where the water flows quickly but is only 5-10cm deep. Here, the population of *S. lacustris* is so dense that a pheromone would not be diluted too much. In all colonies of this species at least some gemmules occurred in addition to larvae. The few reports of larvae in *E. muelleri* and *T. horrida* also originate from populations in stagnant water.

The report of larvae in *E. fragilis* occurring in only one year (1994) suggests that sexual reproduction occurs in some years, even in species without regular sexual reproductive strategies.

Many of the different strategies and life-cycles mentioned above help species avoid competition or enhance their competitive abilities. Competitive interactions among sponges, or between sponges and other organisms, are regularly observed in the field. As shown above, species have their highest abundance at different times of the year (Figs 5-9, Table 2). Many details of life histories can be interpreted as mechanisms to enhance species' competitive abilities, including the fact that during periods of highest abundance of *S. lacustris* the proportion of colonies with symbiotic algae is also considerable (Fig. 5). These symbionts strongly enhance the growth of their host (Frost & Williamson, 1980). In *T. horrida* smaller colonies regularly fuse to form larger ones. Neubert & Eppler (1991) discussed whether the competitive ability was reduced, and therefore *T. horrida* was relatively rare compared to other freshwater species. However, my data show that it was the

most abundant sponge in the Rhine, and is also very competitive among sponges and in competition with other organisms. It is concluded that competition for space is the species' main challenge.

ACKNOWLEDGEMENTS

I thank the Hessische Landesanstalt für Umwelt for making it possible to use the research ship 'Argus', the crew of the ship is acknowledged for their good humour and helpfulness. Mr J. Wittmann kindly provided me with Spongillidae of his collections from 11.05.1994, 08.06.1994 and 30.06.1994. Dr H. Pohl helped me a lot with some figures. I am grateful to an anonymous reviewer, who substantially improved the manuscript. This paper was written during a stay as a postdoctoral fellow in Israel financed by the DAAD.

LITERATURE CITED

- ARNDT, W. 1926. Die Spongillidenfauna Europas. Archiv für Hydrobiologie 17: 337-365.
1928. Porifera, Schwämme, Spongien. Pp. 1-94. In Dahl, F. (ed.) Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und ihrer Lebensweise. Vol. 4. (Porifera - Hydrozoa - Coelenterata - Echinodermata). (Gustav Fischer Verlag: Leipzig).
- BARTL, J. 1984. Biologische, chemische und physikalisch-chemische Bekämpfung von *Ephydatia fluviatilis* (L.) in Industriewasseranlagen. Inaugural-Dissertation der Naturwissenschaftlichen Fakultät. (Justus-Liebig-Universität Gießen: Gießen).
- BISBEE, J.W. 1992. Life cycle, reproduction, and ecology of freshwater sponges in a South Carolina pond. I. Life cycle and reproduction of *Spongilla lacustris*. Transactions of the American Microscopical Society 111(2): 77-88.
- BRONSTED, A. & BRONSTED, H.V. 1953. The effect of symbiotic zoochlorellae on the germination rate of gemmules of *Spongilla lacustris* (L.). Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 115: 133-144.
- CHEATHUM, E.P. & HARRIS, J.P. JR. 1953. Ecological observations upon the fresh-water sponges in Dallas County, Texas. Field & Laboratory 21(3): 97-103.
- CONRATH, W., FALKENHAGE, B. & KINZELBACH, R. 1977. Übersicht über das Makrozoobenthon des Rheins im Jahre 1976. Gewässer und Abwässer 62/63: 63-84.
- CORRIERO, G., VACCARO, P., MANCONI, R. & PRONZATO, R. 1994. Life strategies of *Ephydatia fluviatilis* (L., 1758) in two different environments. Pp. 321-326. In Soest, R.W.M. van, Kempen, T.M.G. van & Braekman, J.-C. (eds) Sponges in time and space. (Balkema: Rotterdam).
- COURRÈGES, V.C. & FELL, P.E. 1989. Sexual and asexual reproduction by the freshwater sponge *Anheteromeyenia ryderi*, with emphasis on spermatogenic activity. Transactions of the American Microscopical Society 108(2): 127-138.
- FRANZ, H.W. 1992. Der Rhein und seine Besiedlung im Wandel: Schwebstoffzehrende Organismen (Hydrozoa, Kämpotozoa und Bryozoa) als Indikatoren für den ökologischen Zustand eines Gewässers. Pollichia-Buch 25: 1-167.
- FROST, H.W. & WILLIAMSON, C. 1980. In situ determination of the effect of symbiotic algae on the growth of the freshwater sponge *Spongilla lacustris*. Ecology 61(6): 1361-1370.
- FROST, T.M., DENAGY, G.S. & GILBERT, J.J. 1982. Population dynamics and standing biomass of the fresh-water sponge *Spongilla lacustris*. Ecology 63(5): 1203-1210.
- GILBERT, J.J. & SIMPSON, T.L. 1976. Gemmule polymorphism in the freshwater sponge *Spongilla lacustris*. Archiv für Hydrobiologie 78(2): 268-277.
- GILBERT, J.J., SIMPSON, T.L. & DENAGY, G.S. 1975. Field experiments on egg production in the fresh-water sponge *Spongilla lacustris*. Hydrobiologia 46(1): 17-27.
- GUGEL, J. 1995. Erstnachweis von *Eumapius carteri* (Bowerbank 1863) (Porifera, Spongillidae) für Mitteleuropa. Lauterbornia 20: 103-110.
- HARSHA, R.E., FRANCIS, J.C. & POIRRIER, M.A. 1983. Water temperature: a factor in seasonality of two fresh-water sponge species, *Ephydatia fluviatilis* and *Spongilla alba*. Hydrobiologia 102: 145-150.
- KINZELBACH, R. 1995. Neozoans in european waters - exemplifying the worldwide process of invasion and species mixing. Experientia 51: 526-538.
- LEVAUX, M. 1941. Contribution à l'étude histologique de l'ovogénèse et de la spermatogénèse des Spongillidae. Annales de la Société Royale de Belgique 1941: 251-269.
1942. Contribution à l'étude histologique de l'ovogénèse et de la spermatogénèse des Spongillidae (Suite). Annales de la Société Royale de Belgique 1942: 33-50.
- MANCONI, R. & PRONZATO, R. 1991. Life cycle of *Spongilla lacustris* (Porifera, Spongillidae). A cue for environment-dependent phenotype. Hydrobiologia 220: 155-160.
- MANN, K.H., BRITTON, R.H., KOWALCZEWSKI, A., LACK, T.J., MATHEWS, C.P. & MCDONALD, I. 1972. Productivity and energy flow at all trophic levels in the river Thames, England. Pp. 579-596. In Kajak, Z. & Hillbricht, A. I. (eds) Productivity problems of freshwaters. Proceedings of the IBP-UNESCO Symposium on Productivity Problems of Freshwaters Kazmierz

- Dolny, Poland, May 6-12, 1970 (UNESCO: Warszawa, Kraków).
- MUKAI, H. 1989. Growth and reproduction in four species of freshwater sponges in their natural surroundings. Science Reports of the Faculty of Education, Gumna University 38: 25-47.
- NEUBERT, E. & EPPLER, G. 1992. *Trochospongilla horrida* (Weltner 1893) - Neufunde aus dem Rhein. Lauterbornia 9: 59-63.
- PENNEY, J.T. & RACEK, A.A. 1968. Comprehensive revision of a worldwide collection of freshwater sponges (Porifera, Spongillidae). United States National Museum Bulletin 272: 1-184.
- PIANKA, E.R. 1970. On r- and K-selection. American Naturalist 104: 592-597.
- PRONZATO, R. & MANCONI, R. 1991. Colonization, life cycle and competition in a freshwater sponge association. Pp. 432-444. In Reitner, J. & Keupp, H.(eds) Fossil and recent sponges. (Springer Verlag: Berlin)
- 1994a. Adaptive strategies of sponges in inland waters. Bollettino di Zoologia 61: 395-401.
- 1994b. Life history of *Ephydatia fluviatilis*. a model for adaptive strategies in discontinuous habitats. Pp. 327-331. In Soest, R.W.M. van, Kempen, T.M.G. van & Brackman, J.-C.(eds) Sponges in time and space. (Balkema: Rotterdam).
1995. Long-term dynamics of a freshwater sponge population. Freshwater biology 35: 485-495.
- PRONZATO, R., MANCONI, R. & CORRIERO, G. 1993. Biorhythm and environmental control in the life history of *Ephydatia fluviatilis* (Demospongiae, Spongillidae). Bollettino di Zoologia 60: 63-67.
- RASMONT, R. 1962. The physiology of gemmulation in fresh-water sponges. Symposium of the Society for the Study of Development and Growth 20: 3-25.
1963. La rôle de la taille et de la nutrition dans le déterminisme de la gemmulation chez les spongillides. Developmental Biology 8: 243-271.
- RÜTZLER, K. 1965. Substratstabilität im marinen Benthos als ökologischer Faktor, dargestellt am Beispiel adriatischer Porifera. Internationale Revue der gesamten Hydrobiologie 50(2): 281-292.
- SCHÖLL, F., BECKER C. & TITTIZER, T. 1995. Das Makrozoobenthos des schiffbaren Rheins von Basel bis Emmerich 1986-1995. Lauterbornia 21: 115-137.
- SCHÖN, A. 1957. Massenentwicklung von Schwämmen in Rheinkraftwerken. Zeitschrift für Fischerei, N.F. 1(6): 85-86.
- SIMPSON, T.L. 1980. Reproductive processes in sponges: a critical evaluation of current data and views. International Journal of Invertebrate Reproduction 2: 251-269.
- STEUSLOFF, U. 1938. Beiträge zur Ökologie nordwestdeutscher Spongilliden. Archiv für Hydrobiologie 33: 309-338.
- TITTIZER, T., SCHÖLL, F. & SCHLEUTER, M. 1990. Beitrag zur Struktur und Entwicklungsdynamik der Benthofauna des Rheins von Basel bis Düsseldorf in den Jahren 1986 und 1987. Pp. 293-323. In Kinzelbach, R. & Friedrich, G. (eds) Limnologie aktuell 1 (Biologie des Rheins). (Gustav Fischer Verlag: Stuttgart).
- VAN DE VYVER, G. & WILLENZ, P. 1975. An experimental study of the life-cycle of the fresh-water sponge *Ephydatia fluviatilis* in its natural surroundings. Wilhelm Roux' Archiv 177: 41-52.
- WEISSENFELS, N. 1989. Biologie und mikroskopische Anatomie der Süßwasserschwämme (Spongillidae) (Gustav Fischer Verlag: Stuttgart)
- WILLIAMSON, C.E. & WILLIAMSON, G.L. 1979. Life-cycles of lotic populations of *Spongilla lacustris* and *Eunapius fragilis* (Porifera, Spongillidae). Freshwater Biology 9: 543-553.